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THE OLDEST FOSSIL PHOLCID AND SELENOPID SPIDERS (ARANEAE) IN LOWERMOST EOCENE AMBER FROM THE PARIS BASIN, FRANCE

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ABSTRACT. Two new spiders, *Quamtana huberi* new species (Pholcidae) and *Selenops* sp. indet. (Selenopidae), are described from Lowermost Eocene (Ypresian) amber from Le Quesnoy, Oise department, Paris Basin, France. Both specimens represent the oldest known fossils of their respective families. This is the first fossil record of the extant genus *Quamtana*, extending its known geological range by 53 Megaannums (Ma). The known geological age of Pholcidae is extended by approximately 5–10 Ma from that of its previous oldest occurrence in Baltic amber. The known age of Selenopidae and the extant genus *Selenops* are extended by approximately 30 Ma, from their previous oldest occurrence in Dominican Republic amber. The distribution of extant species from these genera suggests the inclusions in amber from the Paris deposit have close affinities with the African fauna.

Keywords: French amber, new species, paleontology, Pholcidae, *Quamtana*, Selenopidae, *Selenops*

France has a diverse fossil spider fauna. Both the oldest known mesothele (Selden 1996) and mygalomorph (Selden & Gall 1992) spiders originate from French sediments. Early reports of French fossil spiders include Gourret (1888) and Berland (1939) who described araneomorph Tertiary fossil spiders from Aix en Provence. Spiders in Cretaceous ambers from France have been known for some time (Schlüter 1978; Néraudeau et al. 2002) but these have yet to be described. Recently, Nel et al. (2004) identified a new source of fossil amber spiders from the Lowermost Eocene of Le Quesnoy in the Paris Basin. The presence of the spider family Oonopidae was reported from this deposit by Penney (2006: text-fig. 2) and the specimen was formally described as *Orchestina parisiensis* by Penney (in press). This paper describes two more specimens from this deposit, which represent the oldest known fossils of the spider families Pholcidae and Selenopidae.

GEOLOGICAL SETTING AND PALEOENVIRONMENT

The amber-bearing strata occur under the River Oise Quaternary deposits at Le Quesnoy, Chevrière (49°21′N, 2°41′E), region of Creil, Oise department, France. They prograde toward the northeast and lie at the bottom of two channels, which cut into the underlying Thanetian marine greensands. The Sparnacian beds consist of a succession of lenticular bodies with two main facies: a) clayed sands rich in frequently pyritized lignite, together with amber, and b) grey clayey sands with less lignite and with a continental vertebrate fauna (Nel et al. 2004). A reconstruction of the paleoenvironment was provided by Nel et al. (1999) and summarized by Nel et al. (2004). Based upon the fossils identified to date, Nel et al. (2004) concluded that 53 Myr ago the region consisted of a fluvial wet forest surrounded by semi-deciduous or deciduous woodland, in a warm climate with wet and dry seasons.

METHODS

The specimens upon which this paper is based are deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHN). Prior to receipt by the author, the amber piece containing the selenopid had been mounted on a glass microscope slide. All measurements were made using an ocular graticule. Photographs were taken with a Nikon Coolpix 4500 digital camera attached to a Leica M10 stereomicroscope with a 1.6× planapochromatic objective, using a Volpi Intralux 6000 ringlight illuminator inverted on a custom de-

signed base, to produce a 'dark field' effect. CombineZ 5 software was used for computer generation of 3D images, which were then manipulated in Adobe Photoshop. In leg formula (e.g., 1, 2, 4, 3) legs are ranked in order of length, longest first. Abbreviations used in the text and figures: ab = abdomen; ALE = anterior lateral eye; AME = anterior median eye; b = bulb; cda = cheliceral distal apophysis; cla = cheliceral lateral apophysis; cx = coxa; fe = femur; mt = metatarsus; mx = maxilla; p = procursus; pa = patella; PLE = posterior lateral eye; PME = posterior median eye; st = sternum; t = trichobothria; ta = tarsus; ti = tibia; tra = lateral apophysis of palpal trochanter; 1–4 = walking legs 1–4.

SYSTEMATIC PALEONTOLOGY

Family Pholcidae C.L. Koch 1851
Genus *Quamtana* Huber 2003

Type species.—*Quamtana merwei* Huber 2003, by original designation.

Diagnosis.—Long-legged, six- or eight-eyed pholcids with globular, oval or elevated and often posteriorly pointed opisthosoma, varying in total size from 1–4 mm. Distinguished from other genera by the pair of modified hairs on the male cheliceral apophyses (Huber 2003).

Remarks.—This genus is currently known from extant species in sub-Saharan Africa.

Quamtana huberi new species
Figs. 1–3

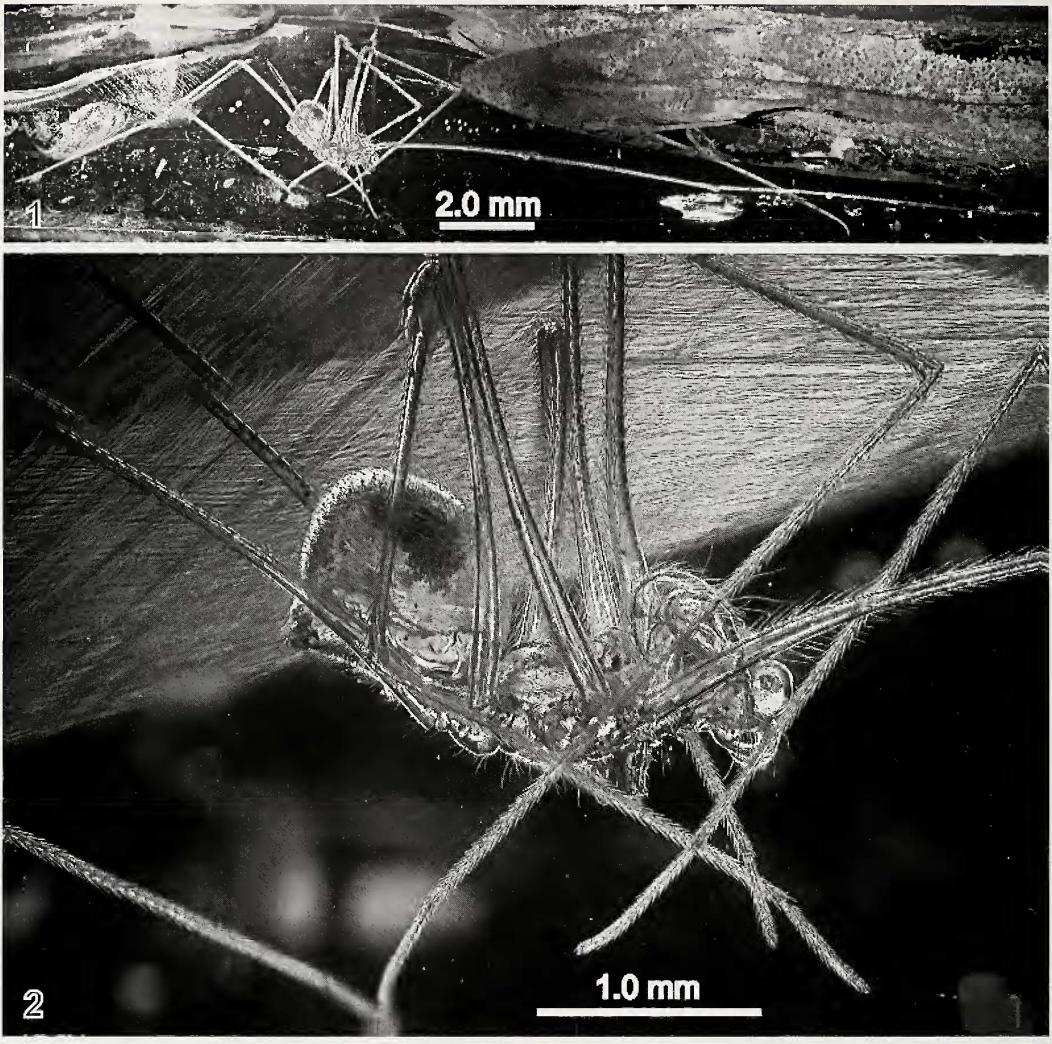
Type material.—Holotype male, Lowermost Eocene amber, Le Quesnoy (49°21′N, 2°41′E), Oise department, Paris Basin, France (MNHN PA 3148).

Etymology.—The specific epithet is a patronym in honor of Dr. Bernhard A. Huber in recognition of his excellent contributions to pholcid spider taxonomy and systematics.

Diagnosis.—The structure of the palpal procursus when examined in retrolateral view distinguishes the new species from all extant species, by the combination of an anteriorly directed finger-like projection located immediately below a posteriorly directed flap-like apophysis.

Description.—Body length 1.58 mm, carapace visible only in lateral view, 0.58 mm long, without any distinguishing features (Figs. 1–3). At least six subequal eyes present in two triads (Figs. 2, 3), the presence or absence of the AME cannot be determined because this region of the carapace, including the clypeus is not clearly visible. Sternum 0.38 mm long. Each chelicera with a proximal lateral apophysis, a proximal anterior apophysis and a distal anterior apophysis with modified hairs (Fig. 3). The presence or absence of a sclerotized cone associated with the distal cheliceral apophysis cannot be determined, but this character is often difficult to observe in Recent specimens and usually requires SEM (Huber 2003). Abdomen globular 1.00 mm long, 0.75 mm high (Figs. 1–3). Legs long (Fig. 1), formula 1,2,4,3; leg 1 fe 4.00 mm, pa 0.25 mm, ti 3.83 mm, mt 5.75 mm, ta 0.98 mm, total 14.81 mm; leg 2 fe 2.50 mm, pa 0.25 mm, ti 2.08 mm, mt 3.00 mm, ta 0.68 mm, total 8.51 mm; leg 3 fe 1.75 mm, pa 0.20 mm, ti 1.35 mm, mt 2.00 mm, ta 0.48 mm, total 5.78 mm; leg 4 fe 2.45 mm, pa 0.23 mm, ti 2.00 mm, mt 2.73 mm, ta 0.48 mm, total 7.89 mm; all lacking spines. Each mt with a trichobothrium located one tenth of the way along from the proximal end of the segment. There also appear to be a maximum of two trichobothria in the proximal region of each ti, although these may be erect setae. Pedipalp, trochanter with a distinct retrolateral apophysis, femur widening distally and patella subtriangular, both without visible modifications. Tibia expanded proximally, narrowing distally, with two trichobothria and two long setae distally. Procursus with an anteriorly directed finger-like projection located immediately below a posteriorly directed flap-like apophysis, distal region not visible; bulb globular, attached prolaterally (Fig. 3).

Remarks.—The new species is tentatively placed in *Quamtana* rather than *Spermophora* Hentz 1841, but this assignment is somewhat problematic due to the invisibility of certain structures in the sole specimen and the absence of females. For example, the chelicerae of male *Quamtana* have a very distinctive pair of modified (pointed, conical) hairs imbedded in the tip of the cheliceral apophyses. The core group of *Quamtana* has an even more distinctive projection of the apophysis accompanying the modified hairs. *Spermophora* has either two or three globular hairs or no modified hairs on the male chelicerae (Huber 2005). The shape of the modified hairs in the fossil specimen cannot be resolved. The proximal



Figures 1–2.—*Quamtana huberi* new species, holotype male, MNHN PA 3148, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France: 1. Lateral view of whole specimen; 2. Lateral view of body region.

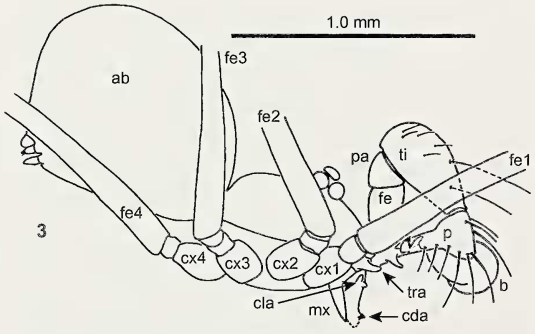


Figure 3.—*Quamtana huberi* new species, holotype male, MNHN PA 3148, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France.

apophyses in the fossil also deserve consideration. It is extremely unusual for pholcids to have two apophyses proximally (Fig. 3), and one case is *Spermophora senoculata* (Dugès 1836). No other *Spermophora* or *Quamtana* species are known to possess two proximal apophyses (B.A. Huber pers. comm. 2005).

In *Quamtana* the palpal bulb sits prolaterally on the tarsus, i.e., looking at the palp ectally the bulb does not project dorsally beyond the tarsus. However, in the fossil the bulb appears to be in a dorsal position. The problem with this character is that the bulb may rotate as an artifact of fixation, such that a prolaterally attached bulb may end up in a dorsal po-

sition (B.A. Huber pers. comm.). *Quamtana* belongs in a group of genera with a very strong sclerite connecting the bulb to the tarsus, but in true *Spermophora* this sclerite is absent. Unfortunately, the relevant region is not visible in the fossil. A ventral flap on the procursus occurs in most *Spermophora* species, but is not known in *Quamtana*. In the core group of *Spermophora*, this flap is sclerotized and serrated (Huber 2005). The fossil possesses a flap similar to *Spermophora* outside the core group. However, *Spermophora* have very distinctive bulbal projections: a serrated apophysis, a hooked apophysis and the embolus. In *Quamtana* there is more variation, but no species is known with a serrated bulbal apophysis (Huber 2003). In the fossil specimen, no bulbal projections can be seen, which argues against placement in *Spermophora*. It can be expected that discovery of new fossil specimens will help resolve the above concerns regarding whether or not the species is correctly placed in *Quamtana*.

Family Selenopidae Simon 1897
Genus *Selenops* Latreille 1819

Type species.—*Selenops radiatus* Latreille 1819 by monotypy.

Diagnosis.—*Selenops* differs from other selenopid genera by the arrangement of the eyes. The AME, PME and ALE aligned or slightly recurved, with the PME equal or subequal in size to AME. Leg 2 > leg 4; ti and mt 1–2 with three, and two pairs of ventral spines respectively (Corronca 2002).

Remarks.—*Selenops* is an extant genus and has been recorded from many parts of the world including the Mediterranean region, Africa, Asia, Australia and the Americas (Platnick 2005).

Selenops sp. indet.
Figs. 4–6

Material examined.—1 juvenile, Lowermost Eocene amber, Le Quesnoy (49°21′N, 2°41′E), Oise department, Paris Basin, France (MNHN PA 2375).

Description.—Body length 1.81 mm, carapace wider than long: 0.74 mm long, 0.81 mm at its widest point, with rounded sides (Figs. 4, 6), with sparse setae and a prominent ocular region. Eight eyes: AME, ALE and PME in a straight line, PLE set further back (Fig. 6). Clypeus and cheliceral structure and dentition not visible. Maxillae longer than wide, labium wider than long, sternum subcircular (Fig. 5), 0.51 mm diameter. Abdomen longer (1.07 mm) than wide (0.59 mm) (Figs. 4, 5), lacking the tufts of white hairs present in some extant species; spinnerets unmodified.

Legs long, laterigrade, formula 2,3,4,1; leg 1 fe 0.57 mm, pa 0.23 mm, ti 0.41 mm, mt 0.24 mm, ta 0.27 mm, total 1.72 mm; leg 2 fe 0.79 mm, pa 0.29 mm, ti 0.57 mm, mt 0.43 mm, ta 0.33 mm, total 2.41 mm; leg 3 fe 0.69 mm, pa 0.29 mm, ti 0.56 mm, mt 0.41 mm, ta 0.31 mm, total 2.26 mm; leg 4 fe 0.71 mm, pa 0.21 mm, ti 0.50 mm, mt 0.40 mm, ta 0.29 mm, total 2.11 mm. The extremely juvenile nature of the specimen makes it impossible to differentiate between true leg spines and other leg setae. Each ti, mt and ta with long trichobothria (Figs. 4–5), tarsi with two claws, prolateral claw distinctly more pectinate than retrolateral claw. Pedipalps unmodified.

Remarks.—Although only a juvenile, this specimen clearly belongs in *Selenops* based on the eye arrangement (Fig. 6), the general habitus and in having legs 2 > legs 4 (Figs. 4, 5).

DISCUSSION

Pholcidae is one of the most diverse spider families with 871 extant species in 75 genera (Platnick 2005), however Huber (2003) estimated that this may represent no more than perhaps 10% of their total global biodiversity. Fossil pholcids are common in Miocene amber from the Dominican Republic, with ten named species described from one fossil genus and three extant genera (Penney & Pérez-Gelabert 2002; Wunderlich 2004). Previous reports of fossil Pholcidae in Baltic amber were discussed by Wunderlich (1986, 2004), but the first unequivocal description of the family from that deposit was by Wunderlich (2004) who described two new species in a new fossil genus. The new species described above represents the oldest fossil record of the extant family Pholcidae, extending its known geological range by approximately 5–10 Ma. This is the first fossil record of the extant genus *Quamtana*, extending its known geological range by 53 Ma. Extant species of *Quamtana* are distributed in sub-Saharan Africa and in South Africa in regions that have > 600 mm annual precipitation (Huber 2003). Though little is known of their behavior and

Figures 4–5.—*Selenops* sp. indet., juvenile, MNHN PA 2375, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France: 4. Dorsal view; 5. Ventral view.

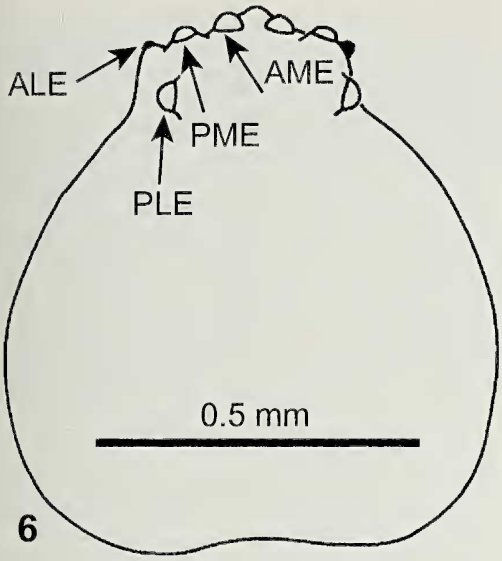


Figure 6.—*Selenops* sp. indet., juvenile, MNHN PA 2375, in Lowermost Eocene amber from Le Quesnoy, Oise department, Paris Basin, France: carapace showing eye arrangement.

ecology, the sparse data available indicate that most extant species live close to the ground, although specimens have been collected by beating vegetation (Huber 2003).

The extant spider family Selenopidae has been described from sub-fossil specimens preserved in Madagascan copal (Bosselaers 2004; Wunderlich 2004; Penney et al. 2005) and from fossil species in Miocene Dominican Republic amber (see Schawaller 1984; Wunderlich 1988, 2004; Penney 2001). However, despite an enormous number (100,000+ Wunderlich, pers. comm. 2004) of Baltic amber fossil spiders studied to date, the family remains unknown from that deposit (e.g., Wunderlich 2004). Thus, the specimen described here more than doubles the known geological age of the family Selenopidae and the extant genus *Selenops*, extending the known geological range of both by approximately 30 Ma.

Both specimens described above belong to extant genera that are highly diverse in Africa today and the extant species of the pholcid genus are restricted to that continent. Thus, the fossil fauna in Lowermost Eocene amber from Paris may have African affinities as occurs with Baltic amber taxa, e.g., the spider family Archaeidae, which has extant species restricted to South Africa and Madagascar. Penney (unpubl. ms.) commented on the absence of Salticidae (jumping spiders) in the Eocene French fauna, in contrast to their frequent occurrence in the Baltic amber fauna. The French amber selenopid described above represents another intriguing difference between these two faunas, which are close both spatially and temporally. However, it would be premature to try and explain these differences until significantly more arthropod taxa have been described from the French deposit, which is currently in the early stages of investigation (Nel 2004).

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